Zootaxa 1250: 53–68 (2006)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

1250

Redescription of *Echinolaophonte armiger* (Gurney) (Copepoda: Harpacticoida) from the Gulf of Mexico

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Abstract

Echinolaophonte armiger (Gurney, 1927) is redescribed from the Texas coast (Gulf of Mexico). The species has a simple but strong dorsal spinous process on the cephalosome and the pairs of minute, spiny processes along the posterodorsal margins of the prosomites and urosomites. This is the first full description of the species since Gurney's (1927) original report from the Suez Canal. The previous reports of *E. armiger* are reconsidered based on new morphological characters revealed in the present study. As a result, *Echinolaophonte hystrix* (Brian, 1928) is revived as a valid species, and the status of closely related species, formerly known as *E. armiger*, is also discussed.

Key words: *Echinolaophonte armiger*, Laophontidae, marine harpacticoid copepods, Gulf of Mexico

Introduction

Since Gurney (1927) described *Echinolaophonte armiger* as *Laophonte armiger* from the Suez Canal, the species has been reported from the Tyrrhenian Sea (Brian 1928; Pesta 1959), Bermuda (Willey 1930), Western Australia (Nicholls 1945), the Brazilian coast (Carvalho 1952), the Caroline Islands (Vervoort 1964), the Californian coast (Lang 1965) and the eastern central Atlantic (Marinov 1977).

In 1941, Nicholls proposed the genus *Echinolaophonte* for several species previously assigned to *Laophonte*, including *L. armiger.* The other species Nicholls (1941) placed in his new genus were: *Laophonte horrida* Norman, 1876 (which he designated the type

Accepted by G. Walker-Smith: 24 May 2006; published: 3 Jul. 2006

species), *Laophonte brevispinosa* Sars, 1908 and *Laophonte mirabilis* Gurney, 1927. In addition, Nicholls (1941) regarded *L. hystrix* Brian, 1928 as a junior-synonym of *E. armiger* without proper explanation. Brian (1929) had previously identified *Laophonte steueri* van Douwe, 1929 as a junior synonym of *L. hystrix*. Lang (1944, 1948) independently reallocated this *horridus*-group to *Onychocamptus* Daday and regarded *L. hystrix* Brian, 1928 as a junior synonym of *E. armiger*. Lang (1965) accepted the establishment of *Echinolaophonte* and described a new form of *E. armiger*: *E. armiger briani* Lang, 1965.

Since then, six species and one subspecies have been added (Bodin 1997) to the genus *Echinolaophonte*: *E. gladiator* (Vervoort, 1964) from the Caroline Islands, *E. armiger briani* from Californian coast, *E. oshoroensis* Itô, 1969 from Japan, *E. tropica* Ummerkutty, 1970 from India, *E. tetracheir* Mielke, 1981 from the Galapagos Islands, and *E. minuta* Cottarelli and Forniz, 1991 and *E. veniliae* Cottarelli, Forniz and Bascherini, 1992 from Italy.

Gurney's (1927) original description of *Laophonte armiger* described the simple, dorsal spiny process on the cephalothorax and the less complex ornamentation on the dorsal surface of prosome and urosome, although others (Lang 1965; Vervoort 1964) reported *E. armiger*'s complex ornamentations in the cephalothorax and the dorsal body surface. Considering *E. armiger*'s exceptionally wide distribution from the Suez Canal to Western Australia and the Brazilian coast, as well as the polymorphic body ornamentations, its status as a single species needs to be re-evaluated. During a survey of the harpacticoid community in the Gulf of Mexico, *E. armiger* was collected from the Texas coast, U.S.A. and is re-described herein.

Material and methods

Samples were collected off the Texan coast. Detailed information on the sampling process is provided in Lee *et al.* (2003). Specimens were dissected in lactic acid and the body parts were mounted on slides in lactophenol mounting medium. Preparations were sealed with Glyceel or transparent nail varnish. All drawings have been prepared using a drawing tube on a Leica DMLB differential interference contrast microscope.

The descriptive terminology is adopted from Huys *et al.* (1996). Abbreviations used in the text are: A1, antennule; A2, antenna; ae, aesthetasc; exp, exopod; enp, endopod; P1–P6, first to sixth thoracopod; exp(enp)-1(2, 3) to denote the proximal (middle, distal) segment of a ramus. Specimens are deposited in The Natural History Museum, London (NHM). The syntypes of *E. armiger* were loaned from the NHM and Vervoort's samples of *E. armiger* and *Echinolaophonte gladiator* came from the National Museum of Natural History, Smithsonian Institute. Length of scale bars (in figures) are given in μm.

Family Laophontidae T. Scott, 1905

Genus *Echinolaophonte* Nicholls, 1941

Echinolaophonte armiger (Gurney, 1927)

(Figures 1–6)

Laophonte armiger Gurney, 1927: 554–556, Fig. 159; Willey, 1930: 108–109, Figs 65–67; Carvalho, 1952: 159–160, Pl. II, Figs 68–71.
Onychocamptus armiger: Lang, 1948: 1423–1424, Abb. 571(12), 580.

Type locality. Port Taufiq, Suez Canal, Egypt.

Material examined

Syntypes: (NHM 1928.4.2.121) 1♀ dissected on 12 slides, permission to dissect syntype granted by NHM and 2 ♀♀ in 70% alcohol, from Toussoum, Suez Canal, Cambridge Suez Canal Expedition 1924. Other material: 1♀ dissected on 12 slides (NHM 2003-114), and 1♂ dissected on 11 slides (NHM 2003-115), all from MI686 (37°50'46" N, 31°31'35" W), off Texas coast, Gulf of Mexico, depth 40 m, 22 April 2000, collected by W. Lee.

Description

FEMALE. Total body length 618 μm (measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at about 1/3 from posterior margin of cephalic shield: 182 μm. Urosome gradually tapering posteriorly (Fig. 1A).

Cephalothorax with smooth posterior margin; lateral posterior side of cephalic shield swollen making triangular expansions at both sides. Pleural areas well developed and rounded without lobate posterolateral angles. Entire surface covered with tiny denticles [expressed as dots] as illustrated in Fig. 1A–B. Sensillae and few pores present as illustrated in Fig. 1A–B. Strong, dorsal, spinous process present at median posterior margin; extending to middle of P2 bearing somite (Fig. 1A). Dorsal median ridge present at cephalothorax. Rostrum rectangular-shaped (Fig. 1A), with flat anterior margin, completely fused to cephalosome, with pair of sensillae near anterior margin.

Pedigerous somites covered with minute denticles. All prosomites without defined hyaline frills, hind margin smooth. Each pedigerous somite with row of spinules near posterodorsal margin. P3–P5 bearing somites armed with 1 or 2 pair of protuberances within row of spinules near the posterior margin; 1, 2 and 2, respectively. Body slightly constricted between individual somites.

Urosome (Figs 1A–B, 5A–B) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. All urosomites covered with small denticles

dorsally and laterally. Genital double-somite and its succeeding somite with 1 pair of spiny processes on posterodorsal margin. Ventral surface of urosomites not markedly wrinkled, ventral hind margin with large spinules laterally and medially. Hyaline frills of urosomites not distinct. Genital double-somite (Figs 1A–B, 5A–C) with transverse, surface ridge dorsally and laterally, indicating original segmentation; completely fused ventrally. Genital double-somite with additional pair of spiny dorsal processes on its surface, ridge formed originally from 2 anterior urosomites. Genital field located near anterior margin (Fig. 5A) with very small copulatory pore located in median depression (Fig. 5C). P6 with small protuberance bearing 2 bare setae, outer seta longer than inner seta; with small blunt process next to inner seta. Pseudoperculum well developed, with pair of digitate processes reaching to middle of anal somite (Fig. 5B). Anal somite (Fig. 5B) with smooth, thin operculum flanked by pair of sensillae.

Caudal rami (Fig. 5A–B) short, cylindrical, 1.4 times longer than wide; each ramus with 7 setae: seta I bare, shortest; setae II and III bare, subequal at length; setae IV and V fused basally, and pinnate (seta V broken off, but presumably longest); seta VI bare and small; seta VII tri-articulate at base. Each ramus with spinules on dorsal surface. Additional spinular ornamentation present along outer margins and around ventral hind margin. Small tube pore present near dorsal anterior margin.

Antennule (Fig. 2A) 6-segmented, with well developed sclerite around base of segment 1. Segment 1 covered with long spinules. Segment 2 covered with tiny spinules; largest, with small blunt process along the outer margin dorsally. Segment 4 with aesthetasc fused basally to seta and set on distinct pedestal. Armature formula: 1-[1], 2-[7 + 1 pinnate], 3-[6], 4-[1 + (1 + ae)], 5-[1], 6-[9 + trithek]. Apical trithek consisting of small aesthetasc fused basally to 2 bare setae.

Antenna (Fig. 2B) 3-segmented, comprising of coxa, allobasis, free 1-segmented endopod and 1-segmented exopod. Coxa small, with row of spinules. Allobasis elongate, without distinct surface sutures marking original segmentation, with abexopodal pinnate seta near distal margin. Exopod small, about 3 times longer than wide, with 4 well developed, pinnate setae (2 laterally, 2 apically). Row of spinules along lateral margin posteriorly. Endopod slightly shorter than allobasis, lateral armature arising in distal half, consisting of small, bare seta flanked by 2 strong, pinnate spines. Apical armature consisting of 1 pinnate and 1 bare spine, and 3 geniculate setae (outermost geniculate seta fused basally to short seta). Endopod with 2 rows of long spinules laterally and 2 transverse hyaline frills subapically.

Labrum with spinular ornamentation and covered with tiny spinules as in Fig. 5D.

Mandible (Fig. 2D) with well developed gnathobase bearing several multicuspidate teeth around distal margin and pinnate spine at dorsal corner, and with blunt process near distal margin. Palp small, endopod and exopod fused to basis, represented by small peduncles bearing 3 and 1 pinnate setae, respectively. Basal armature represented by pinnate seta.

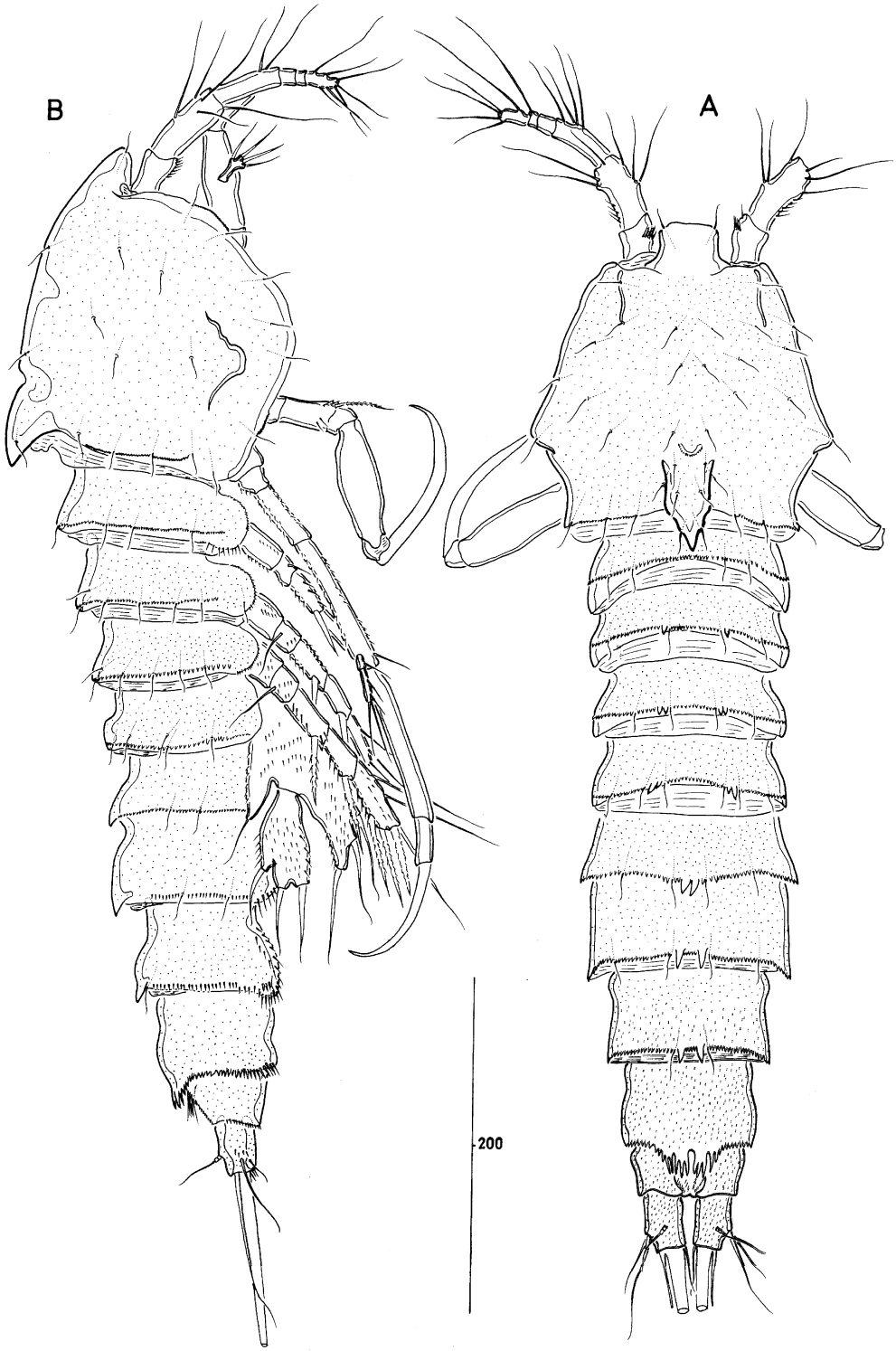

FIGURE 1. *Echinolaophonte armiger* (Gurney, 1927) (♀, NHM 2003-114). A, habitus, dorsal; B, habitus, lateral.

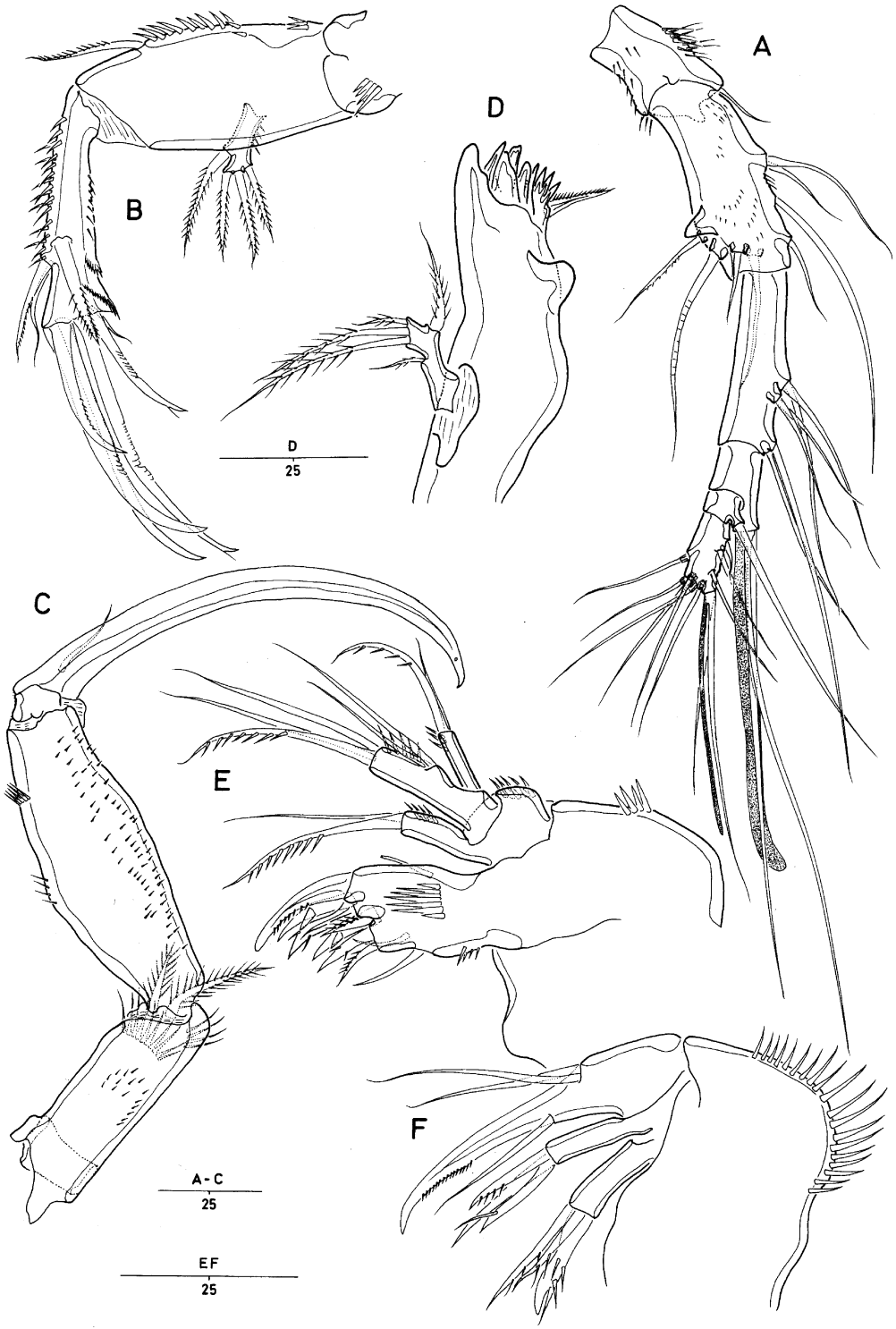

FIGURE 2. *Echinolaophonte armiger* (Gurney, 1927) (♀, NHM 2003-114). A, antennule; B, antenna; C, maxilliped; D, mandible; E, maxillule; F, maxilla.

FIGURE 3. *Echinolaophonte armiger* (Gurney, 1927) (♀, NHM 2003-114). A, P1, anterior; B, P2, anterior; C, P5, anterior.

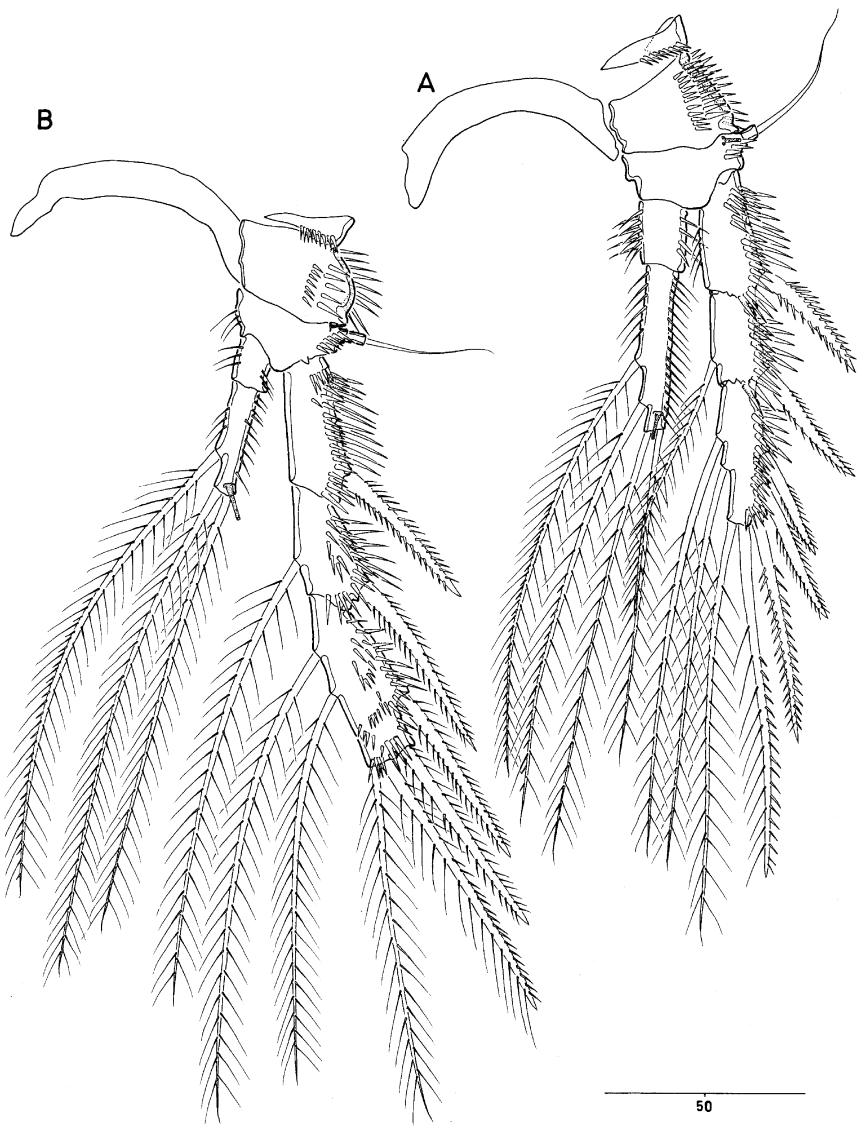

FIGURE 4. *Echinolaophonte armiger* (Gurney, 1927) (♀, NHM 2003-114). A, P3, anterior; B, P4, anterior.

Paragnaths (not figured) strongly developed lobes with medially directed hair-like setules, separated by medial lobe covered with dense pattern of short setules.

Maxillule (Fig. 2E). Praecoxa with few spinules around outer margin. Arthrite strongly developed, with naked seta on anterior surface and 9 spines/setae around distal margin. Row of long spinules on posterior surface, and row of small spinules on inner margin of arthrite. Coxa with cylindrical endite bearing naked seta and curved, pinnate spine, with spinule row on anterior surface, and several long spinules around outer margin. Basis with cylindrical endite bearing 2 naked setae and curved, pinnate spine, with several spinules around outer distal margin. Endopod incorporated in basis, forming small

peduncle with 2 naked setae. Exopod 1-segmented, with 1 pinnate and 1 naked seta apically and few spinules laterally.

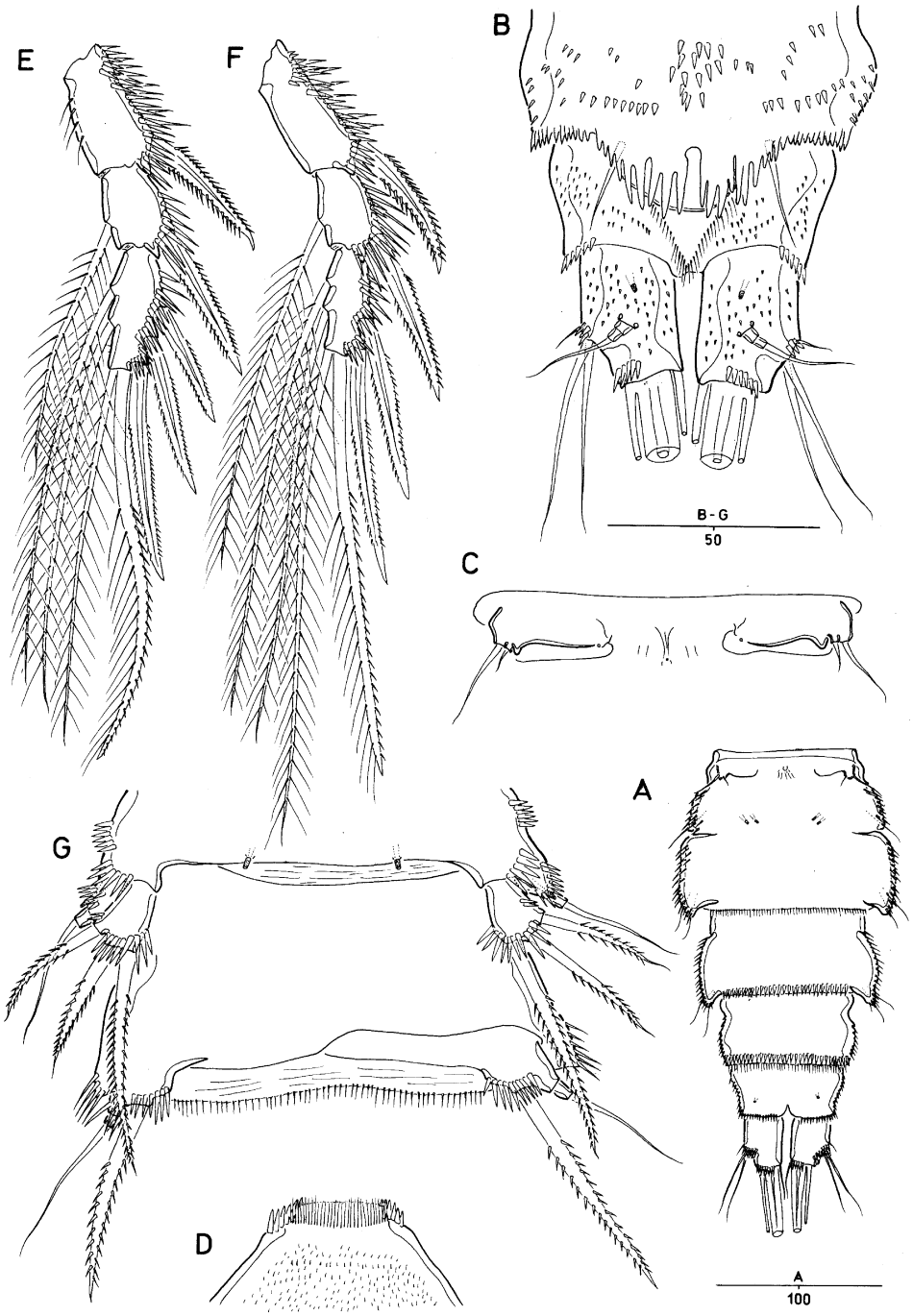

FIGURE 5. *Echinolaophonte armiger* (Gurney, 1927) (♀, NHM 2003-114). A, urosome, ventral view [excluding P5 bearing somite]; B, anal segment and caudal rami, dorsal; C, genital field; D, labrum. E–G (♂, NHM 2003-115), E, P3 exopod; F, P4 exopod; G, P5 and P6.

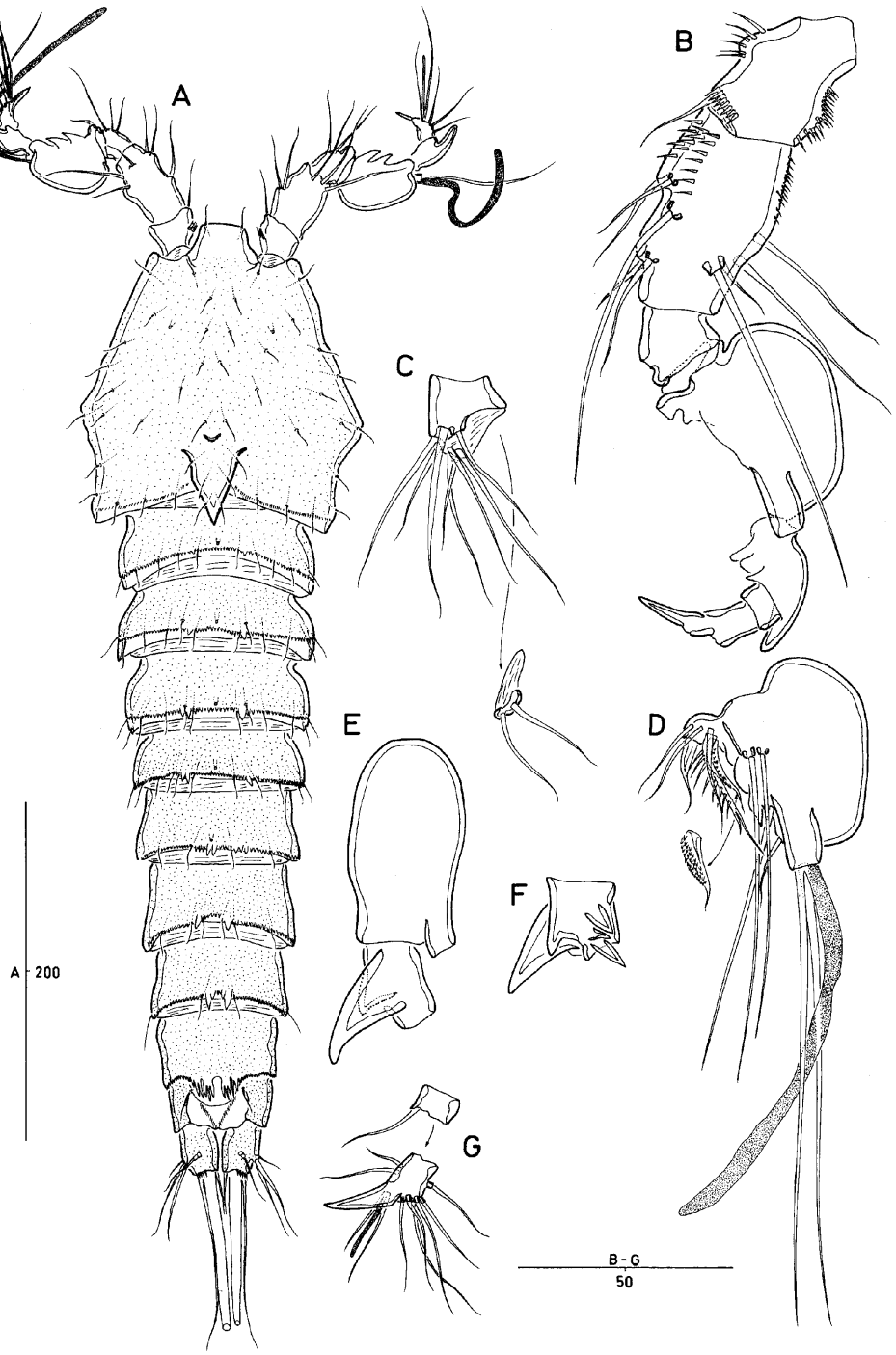

FIGURE 6. *Echinolaophonte armiger* (Gurney, 1927) (♂, NHM 2003-115). A, habitus, dorsal; B, antennule [armature of segments 3–8 omitted]; C, antennular segments 3–4; D, antennular segment 5; E, antennular segments 5–6, posterior; F, antennula segment 6, anterior; G, antennular segments 7–8.

Maxilla (Fig. 2F). Syncoxa with 2 endites, with row of long spinules along outer margin. Each coxal endite cylindrical with 3 pinnate spines respectively. Allobasis drawn out into strong, slightly curved, distally pinnate claw; accessory armature consisting of naked seta on anterior surface. Endopod represented by 2 naked setae.

Maxilliped (Fig. 2C) with 2 plumose setae and several patches of spinules on syncoxa. Basis with 2 rows of spinules along outer margin and tiny spinules along palmar margin and surface. Endopod drawn out into long, naked claw, with short, naked seta at base.

Swimming legs P1–P4 (Figs 3A–B, 4A–B) with wide intercoxal sclerites and well developed praecoxae bearing row of spinules along distal margin. Coxae and bases with anterior rows of surface spinules as figured. Exopods 3-segmented, endopods 2-segmented except in P1. P1 exopod 2-segmented.

P1 (Fig. 3A). Coxa large, with several spinular rows and patches as figured. Anterior tube pore present near articulation with basis. Basis with strong, bipinnate spine on distal pedestal, long setules along inner margin and stout, bipinnate spine and spinules along outer margin. Anterior surface covered with spinules. Exopod small. Exp-1 with unipinnate spine. Exp-2 with 3 unipinnate spines and 2 geniculate setae. Enp-1 4 times as long as exopod, with short spinules along distal outer margin. Enp-2 with strong, denticulate claw and small, naked seta at base.

P2–P4 (Figs 3B, 4A–B). Coxae and bases with spinular rows along outer margin and anterior surface. Basis with tube pore on anterior surface. Outer margin of basis with bipinnate spine (P2) or naked seta (P3–P4); arising from setophore in P3–P4. All segments with pattern of spinules as figured. Inner margins of exopod and endopod segments with long setules or spinules. Tube pore present near distal margin of enp-1 in P2 and enp-2 in P3–P4. P2 enp-2 1.25 times longer than enp-1, endopod reaching to middle of exp-3, and exp-1 longest. P3 enp-2 2.5 times longer than enp-1, endopod reaching to proximal third of exp-3, and exp-3 longer than exp-1. P4 enp-2 2.2 times longer than enp-1, endopod reaching to proximal margin of exp-2, and exp-3 longer than exp-1. Spine and setal formulae as follows:

	Exopod	Endopod
P2	0.1.122	0.120
P3	0.1.223	0.220
P4	0.1.222	0.120

P5 (Fig. 3C) exopod and baseoendopod separate; each covered with spinules as figured. Baseoendopod forming short, outer setophore bearing basal seta and tube pore near proximal area of setophore. Endopodal lobe not reaching to distal margin of exopod, with 1 apical and 3 lateral, pinnate setae; tube pore near base of exopod. Exopod elongate, about 2 times longer than wide, with 3 pinnate setae, each seta arising from distinct cylindrical process.

MALE. Body length 565 μm. Largest width measured at about 1/3 from posterior margin of cephalic shield: 168 μm. Urosome distinctly narrower than prosome (Fig. 6A).

Prosome (Fig. 6A) 4-segmented, comprising cephalothorax and 3 free pedigerous somites. Entire surface covered with tiny denticles as in ♀. Strong dorsal median spinous process present near posterior margin, extended to middle of P 2 bearing somite (Fig. 6A). Rostrum rectangular-shaped (Fig. 6A), with flat anterior margin, completely fused to cephalosome, and with pair of sensillae near anterior margin. Urosome (Fig. 6A) 6-segmented, comprising P5-bearing somite, genital somite and 4 abdominal somites.

Antennule (Fig. 6B–G) 8-segmented and subchirocer with geniculation between segments 5 and 6. Segment 1 covered with several rows of long spinules. Segment 2 without small knob on dorsal surface. Segment 4 represented by small sclerite along anterior margin (inserted in Fig. 6C). Segment 5 swollen. Segment 6 with 3-dimensional process as in Fig. 6E–F. Segment 8 with triangular distal half. Segmental homologies: 1-I, 2-(II-VIII), 3-(IX-XII), 4-XIII, 5-(XIV-XX), 6-(XXI-XXII), 7-XXIII, 8-(XXIV-XXVIII). Armature formula: 1-[1], 2-[9], 3-[8], 4-[2], 5-[8+1 pinnate+2 modified+(1 + ae)], 6-[5 spinous processes], 7-[1], 8-[8+trithek]. Apical trithek consisting of minute aesthetasc and 2 naked setae.

P2–P4 (Fig. 5E–F). Intercoxal sclerites and protopods as in ♀, with surface ornamentation as figured. Exopodal segments slightly bent toward endopod. Endopods without sexual dimorphism. P2 without distinct sexual dimorphism. P3 exopod (Fig. 5E) slightly bent inwards, exp-1 as long as exp-3, outer and distal spines of exopod slightly thicker than in ♀. P4 exopod (Fig. 5F) slightly bent inwards, exp-1 longer than exp-3, outer spines of exp-2 and -3 and distal spine of exp-3 thicker than in ♀.

P5 (Fig. 5G) fused medially, defined at base. Baseoendopod with short, small setophore bearing outer basal seta, and obsolete endopodal lobe represented by tube pore along medial margin, with another tube pore near articulation with setophore. Several rows of coarse spinules along outer margin, and near articulation with exopod. Exopod slightly longer than maximum width, with 3 pinnate setae and several large spinules on anterior surface.

P6 (Fig. 5G) asymmetrical, represented on both sides by small plate: fused to ventral wall of supporting somite along right side, articulating at base and covering gonopore along left side. Outer distal corner produced into cylindrical process bearing few spinules, 1 bipinnate inner and 1 naked outer seta. Outer seta arising from setophore.

Discussion

Present specimens from the Texan coast were identified as *Echinolaophonte armiger* by careful comparison with the three type specimens (NHM 1928.4.2.121). *Echinolaophonte armiger* has simple body ornamentations and a relatively short and simple dorsal process on the cephalothorax (see fig. 1A–B). The simple but strong, dorsal spinous process on the

cephalosome was figured precisely in Gurney's (1927) original description (p. 555, fig. 159A). All other characters of the female including the armature formula of the swimming legs, surface ornamentations, length/width ratios of body segments and the mouthpart structures were shared by the syntypes and the Texan specimens. Gurney (1927) only described the female of *E. armiger.* The male of *E. armiger* was first described by Willey (1930). The absence of any sexual dimorphism in the endopods of P3 is common in *Echinolaophonte* species, however the male specimen from the Texan coast exhibited slightly modified P3 and P4 exopods (Fig. 5 E–F). Willey (1930) also reported the modification of swimming legs in the male, and mentioned that the exopods of P3 and P4 in the male were slightly thickened, and the outer spines somewhat stronger that those in the female.

Based on the observation of the syntypes and the Texan specimens, *Echinolaophonte armiger* is clearly re-defined by: 1) the smooth apical margin of the rostrum, 2) the simple dorsal spinous process on the cephalosome, 3) the armature formula of the swimming legs, 4) the short enp-2 of P2–P4, 5) the unmodified P3 endopod in male, 6) the slightly modified exopods of P3 and P4 in male, 7) the setophore armed the outer basal seta of P5 is short (viz. very long in *E. armiger* f. *briani*), 8) short caudal ramus (only 1.4 times longer than wide, while nearly two times longer than wide in *E. armiger* f. *briani* and *E. hysterix*), 9) the shape of dorsal spiny processes in the prosome and urosome and 10) the shape of pseudoperculum.

Since Gurney (1927) first described *Echinolaophonte armiger* as *Laophonte armiger* from the Suez Canal, several other authors have reported this species from various locations. Most of the species belonging to *Echinolaophonte* have elaborate setular ornamentation on the proximal regions of the dorsal process (Lang 1965: 510, fig. 280c). However, *E. armiger* only has a simple but strong dorsal process on the cephalosome and is easily distinguished from its congeners by the absence of this setular ornamentation. Thus it is assumed that only a few of the previous reports of *E. armiger* actually refer to *E. armiger sensu* Gurney, 1927.

Willey (1930) recorded the male of *L. armiger* from Bermuda and his descriptions of sexual dimorphism in the male, the lateral habitus, and the seta formula of the swimming legs are matched with the present Texan specimens, although there are uncertainties in other characters because of the incomplete descriptions.

Carvalho's (1952) provided a habitus drawing of a female *L. armiger* (Pl. II, Fig. 68), which shows a short dorsal spinous process and triangular expansion of the cephalothorax thus this is considered the third report of *E. armiger sensu* Gurney, 1927. The present report, from off the Texan coast, is the fourth of *E. armiger sensu* Gurney, 1927. Apart from these four reports, all other previous works that mention *E. armiger* are considered to refer to a different species.

Lang (1965) redescribed *E. armiger* f. *typica* from samples donated by Professor A. Brian (p.5 in Lang, 1965), who had originally described *L. hystrix* from the Tyrrhenian Sea

(Brian, 1928). While Lang (1944, 1948) believed *L. hystrix* was a junior synonym of *L. armiger*, his redescription (Lang, 1965) of *E. armiger* f. *typica* was more similar to Brian (1928)'s original description of *L. hystrix* than to *E. armiger sensu* Gurney, 1927.

Laophonte hystrix shows elaborate setular ornamentation on the proximal regions of the dorsal process on the cephalothorax as figured in Lang (1965: 515, fig. 284) in contrast with the simple spinous process of *E. armiger*. In addition, *L. hysterix* also can be differentiated from *E. armiger* by: 1) the shape of rostrum (reverse trapezoid in *L. hysterix*, rectangular in *E. armiger*), 2) body ornamentations, 3) P4 endopod shorter than the exp-1 and 4) smaller body size (*L. hystrix*: 580 in ♀ and 490 in ♂ of Brian, 1928; *E. armiger*: 618 in ♀ and 565 in ♂ of present study, 650 in ♀ of Gurney, 1927), and therefore is reinstated herein as a valid species: i.e. *E. hystrix* (Brian, 1928).

The Californian form, *Echinolaophonte armiger* f. *briani*, needs to be reevaluated as a similar but distinct species to *E. armiger* f. *typica* (viz. *L. hystrix*). These species are clearly distinguished by differences in the body ornamentation (see Lang 1965: pp. 513, 515, figs 282, 284) and the length of the caudal ramus, which is much longer in f. *briani* than in f. *typica*. The combination of these character states, and the remote distribution between both forms indicate these are two separate species. However, the status of both forms can only be confirmed after observation of the type specimens, which is the subject of a future study.

Echinolaophonte armiger sensu Vervoort, 1964 has two outer spines on the P3 exp-3 instead of three as in *E. hystrix* and should be upgraded to a separate species. To confirm the status of *E. armiger sensu* Vervoort, 1964 further observations of the specimens is essential. Unfortunately we were unable to check the dorsal ornamentation of the type specimens (USNM 109730 & 109740) since they had been mounted on glass slides without the cephalothorax. The elevation of *E. armiger sensu* Vervoort, 1964 to species rank is delayed until reexamination of undamaged specimens. Nicholls (1945) reported *E. armiger* from Western Australia and his specimen also had two outer spines on the P3 exp-3 as in Vervoort's (1964) *E. armiger*. Presumably Nicholls's *E. armiger* belongs to *E. armiger sensu* Vervoort, 1964.

Krishnaswamy (1957) reported *E. armiger* from the Madras coast. This species is clearly different from *E. armiger sensu* Gurney, 1927 as it has a bifid rostrum, a narrow median process on the cephalothorax, a shorter and broader P1 exopod and endopod and a relatively large P5 exopod. Krishnaswamy's (1957) specimen seems to belong a distinct species which is superficially similar to *E. hystrix*.

Pesta (1959) reported *Onychocamptus armiger* from the Tyrrhenian Sea but the P4 exp-3 of his male specimen only had one outer spine, which is a characteristic unknown in any other species within the *Echinolaophonte*. Because of the absence of a sexually dimorphic P3 endopod in the male and the elaborate dorsal process on the cephalosome, Pesta's (1959) specimen seems quite similar to *E. hystrix*. Further detailed information is needed to decide on the status of Pesta's report.

Echinolaophonte armiger f. *typica* was reported from Italy, near the type locality of *E. hystrix* (Cottarelli & Forniz 1991; Cottarelli *et al*. 1992). The specimen recorded by Cottarelli *et al*. (1992) is presumably *E. hystrix* due to the presence of the dorsal spinous process of cephalothorax and the pattern of body ornamentations. In addition, Marinov's (1977) report of *Onychocamptus armiger* from the eastern central Atlantic cannot be confirmed because of its incomplete description.

Given the likely misidentification *E. armiger* in many of the published records, the distribution area of *E. armiger* (*sensu* Gurney, 1927) is now considered to be limited to the Suez Canal (i.e. the type locality), the Texan coast (U.S.A.), and possibly Bermuda (Willey, 1930) and the Brazilian coast (Carvalho, 1952).

Acknowledgements

This work was supported by Korea Science and Engineering Foundation (R01-2002-000-00081). Authors thank the crew of R/V *Longhorn* (The University of Texas at Austin, Marine Science Institute), Dr. M. Ma, Mr. R. Kalke, and Mr. L. Hyde for their help in collecting the samples and support during the study period. Authors express special thanks to Ms. Miranda Lowe and Ann Morgan in the Natural History Museum London and Mr. Chad Walter in the Smithsonian Institution for their help with the loan of type material. Authors also thank to Dr. Genefor Walker-Smith and two anonymous reviewers for their critical comments, which help improve the manuscript.

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